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A new species of sand-dwelling catfish, with a phylogenetic diagnosis of *Pygidianops* Myers (Siluriformes: Trichomycteridae: Glanapteryginae)

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A new species of sand-dwelling catfish genus *Pygidianops*, *P. amphioxus*, is described from the Negro and lower Amazon basins. The new species differs from its three congeners in the elongate eel-like body, the short barbels, and the small caudal fin, continuous with the body, among other traits of internal anatomy. The absence of anal fin further distinguishes *P. amphioxus* from all other *Pygidianops* species except *P. magoi* and the presence of eyes from all except *P. cuao*. The new *Pygidianops* seems to be the sister species to *P. magoi*, the two species sharing a unique mesethmoid with a dorsally-bent tip lacking *cornua*, and a produced articular process in the palatine for the articulation with the neurocranium. *Pygidianops amphioxus* is a permanent and highly-specialized inhabitant of psammic environments. Additional characters are proposed as synapomorphies of *Pygidianops*, including a hypertrophied symphyseal joint and associated ligament in the lower jaw; an elongate, laterally-directed, process on the dorsal surface of the premaxilla; and a rotated lower jaw, where the surface normally facing laterally in other glanapterygines is instead directed ventrally. These and other characters are incorporated into a revised phylogenetic diagnosis of *Pygidianops*.

Uma nova espécie do gênero de bagre arenícola *Pygidianops*, *P. amphioxus*, é descrita de diferentes localidades na Amazônia brasileira. A nova espécie difere de seus três congêneres pelo corpo alongado e anguiliforme, pelos barbilhões curtos e pela pequena nadadeira caudal, contínua com o corpo, além de outras características da anatomia interna. A ausência de nadadeira anal distingue *P. amphioxus* de todos os outros *Pygidianops* exceto *P. magoi* e a presença de olhos de todos exceto *P. cuao*. O novo *Pygidianops* parece ser o grupo-irmão de *P. magoi*, as duas espécies compartilhando um mesetmóide com a extremidade dobrada dorsalmente, sem *cornua*, e um processo articular prolongado no palatino para articulação com o neurocrânio. *Pygidianops amphioxus* é um habitante permanente e altamente especializado de ambientes psâmicos. Caracteres adicionais são propostos como sinapomorfias para *Pygidianops*, incluindo uma articulação sinfiseana e ligamento associado hipertrofiados na mandíbula; um processo alongado e dirigido lateralmente na superfície dorsal do pré-maxilar; e a mandíbula rotacionada, de forma que a superfície normalmente lateral em outros Glanapteryginae é dirigida ventralmente. Estes e outros caracteres são incorporados em uma diagnose filogenética revisada de *Pygidianops*.

Key words: Biodiversity, Freshwater, Psammophyly, Systematics, Teleostei.

Introduction

The genus *Pygidianops* was described by Myers (1944) to include a single new species, *P. eigenmanni*. The same paper also described the closely related and equally monotypic *Typhlobelus*. The two genera, along with the previously described *Glanapteryx anguilla* Myers, 1927, formed the Glanapteryginae, a subfamily of Trichomycteridae established in the same publication. The genus *Listrura* was later described by de Pinna (1988) to comprise two species from Southeastern Brazil, the first record of the subfamily outside of the Amazon basin. Since then, all new glanapterygine species fit clearly into one of those four genera. Three additional species of *Listrura* were subsequently described, all from Southeastern Brazilian drainages: *L. tetraradiata* Landim & Costa, *L. boticario* de Pinna & Wosiacki and *L. picinguabae* Villa-Verde & Costa. *Glanapteryx niobium* was described by de Pinna (1998) from an isolated locality in the rio Negro and *Typhlobelus macromycterus* by Costa & Bockmann (1994) from the rio Tocantins. Four additional species, two each of *Pygidianops* and *Typhlobelus*, were described from the río Orinoco drainage by Schaefer *et al.*

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(2005). To date, a total of 14 glanapterygines species have been described, with a number of yet undescribed ones also known to exist. Investigations on phylogenetic relationships of glanapterygines began with Baskin (1973), later complemented and corroborated by de Pinna (1989) and Costa & Bockmann (1994). The genus *Listrura* is considered the sister group to the rest of the subfamily, with *Glanapteryx* as the sister group to *Pygidianops* plus *Typhlobelus*. Additional recent contributions relevant to the knowledge of the subfamily include the comparative anatomy of dorsolateral head muscles in *Listrura* and its phylogenetic placement among representatives of the major clades of Trichomycteridae (Datovo & Bockmann, 2010); morphological trends of glanapterygines (Adriaens *et al.*, 2010), such as body elongation, reduction of appendages, of dark pigmentation and of integumentary teeth (odontodes); and the phylogenetic placement of *Typhlobelus* among representative trichomycterids based on molecular sequence data (Fernández & Schaefer, 2009).

Glanapterygines are among the most peculiar of all catfishes, in both external and internal anatomy. Species of *Pygidianops* and *Typhlobelus* represent perhaps the most extreme instances of psammophilic adaptation in freshwater fishes. The unusual habitats of glanapterygines, reviewed in Nico & de Pinna (1996), Schaefer *et al.* (2005) and Zuanon *et al.* (2006), along with their small size, seem to explain their rarity in museum collections. Such circumstances, in turn, account for the numerous glanapterygines that remain undescribed.

In the present paper we report on a distinctive new species of the genus *Pygidianops*, first discovered inside the forest preserve Adolfo Ducke (maintained by Instituto Nacional de Pesquisas da Amazônia - INPA), but later also found in other Amazonian localities. The species has been mentioned occasionally in the literature and its natural history has been the subject of one academic dissertation (Soares-Carvalho, 2010). In the process of establishing the proper generic assignment of the new form, we disclosed comparative anatomical data relevant to a phylogenetic diagnosis of *Pygidianops*.

Material and Methods

Measurements of SL and its subunits were straight-line, taken with digital calipers. Subunits of HL were measured with an ocular micrometer attached to a stereomicroscope. Definitions of measurements follow Schaefer *et al.* (2005). Cleared and counter-stained specimens were prepared according to slightly modified versions of Taylor & Van Dyke (1985) and Song & Parenti (1995). Nomenclature of cephalic pores of latero-sensory canal system follows Arratia & Huaquin (1995).Counts of vertebrae, ribs and branchiostegal rays were done on cleared and stained specimens only. Vertebral counts do not include those involved in the Weberian complex and the compound caudal centrum (usually considered to consist of PU1+U1, but probably including additional centra) is counted as one. Illustrations were traced from printouts of digitized images obtained by a video camera attached to a stereomicroscope. Additional details were added with the help of a camera lucida attachment on the same equipment. All illustrations were prepared by the first author. Sexing of specimens was based on direct examination of gonads, exposed by a small incision in the abdominal wall, slightly anterior to vertical through anal opening, on the right side of specimens. Abbreviations are: c&s (cleared and stained preparation); MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil); ns (neural spine), and vc (vertebral centrum).

Pygidianops amphioxus, new species
Figs. 1-4

Pygidianops n. sp.; Mendonça *et al.*, 2005: 759 [community ecology].

Pygidianops sp.; Schaefer *et al*., 2005: 5 [comparative material examined]; Soares-Carvalho, 2010 [natural history].

Holotype. INPA 34661, 25.7 mm SL, female, Brazil, Amazonas, Manaus, Reserva Adolfo Ducke, igarapé do Acará, tributary to rio Tarumã, itself tributary to rio Negro, 03°08'S 60°02'W, 10 Nov 1996, A. Kirovsky & M. de Pinna.

Paratypes. All from Brazil. INPA 12427, 4 ex (1 male, 3 females), 23.3-24.8 mm SL (3, 23.3-24.8 mm SL), collected with holotype; INPA 16556, 2 ex (1 female, 1 sex indeterminate), 20.1-27.8 mm SL, same locality as holotype, 25 Nov 2000, F. Mendonça & M. de Pinna; MZUSP 86951, 14 ex (8 males, 6 females), 20.2-28.7 mm SL, Amazonas, rio Preto da Eva, igarapé Sucuriju (trib. to rio Preto da Eva), 14 Aug 2004, M. de Pinna, L. H. Rapp Py-Daniel & L. Sousa; MZUSP 87676, 21 ex (2 c&s, 10 males, 11 females), 23.3-30.4 mm SL (8, 24.0-30.4 mm SL), Amazonas, rio Preto da Eva, igarapé Sucuriju, next to Bom Jesus farm, at km 13 of Ramal Francisca Mendes, 2º45'15.8"S 59º37'29.6"W, 04 Jul 2003, O. Oyakawa *et al.*; MZUSP 105878, 6 ex (all males), 24.2-25.8 mm SL, Amazonas, Manaus, igarapé at Recanto do Chupisco, at side road leaving at km 36 of road Manaus-rio Preto da Eva, 2º49'48.7"S 59º58'11.2"W, 09 Jul 2003, MZUSP team; MZUSP 105879, 3 ex (1 male, 1 female, 1 sex indeterminate), 17.7-25.9 mm SL, same data as INPA 16556; MZUSP 105880, 6 ex (2 c&s, 2 males, 3 females, 1 mutilated), 22.0-26.5 mm SL (3, 22.0-26.5 mm SL), collected with holotype.

Non-type specimens. INPA 31552, 7 ex (1 c&s), 23-25 mm SL, Brazil, Amazonas, Santa Isabel do rio Negro, rio Daraá, rio Negro drainage, cachoeira Panã-Panã, 0°22'15.2"S 64º47'37.6"W, M. S. Rocha & V. L. Masson; MZUSP 104675, 7 ex (3 males, 4 females), 23.7-31.8 mm SL, Pará, Terra Santa, igarapé Jamari (trib. to rio Nhamundá), near Terra Santa, 2º00'03.5"S 56º31'05.1"W, 23 Sep 2009. H. A. Lazzarotto, R. P. Leitão & R. Frederico.

Diagnosis. Distinguished from the three other known species in *Pygidianops* by the caudal fin continuous with the remainder of the body profile (*vs.* caudal fin well differentiated from the body); the elongate body (HL 10-12% SL, *vs*. 16-18%); the relatively even depth of body (*vs*. body markedly less deep close to caudal fin); the short barbels, approximately half as

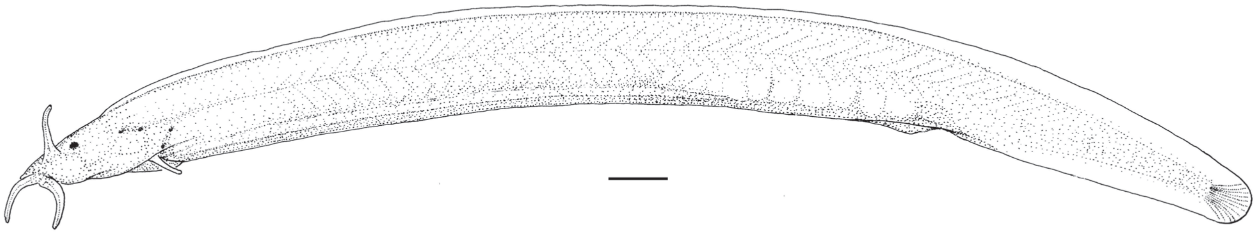

Fig. 1. *Pygidianops amphioxus*, holotype, INPA 34661, female, 25.7 mm SL. Scale bar = 1mm.

long as HL (*vs*. approximately as long as, or longer than, HL); the presence 58 or 59 vertebrae (*vs*. 35-41 in *P*. *magoi*, 41 in *P. cuao*, 37-41 in *P. eigenmanni*); the lack of a lacrimal bone (infraorbital one); the presence of a single continuous ligament connecting the dorsal processes of the premaxillae; and the deep shape of the opercle, resulting from a hypertrophied ascending process. The latter two characteristics are putative autapomorphies for the species. The lack of an anal fin; the presence of a single pair of pleural ribs, the strongly dorsally-deflected tip of the mesethmoid and the lack of mesethmoid cornua further distinguishes *P. amphioxus* from all congeners except *P. magoi*. The presence of eyes separates *P. amphioxus* from all congeners except *P. cuao.*

Description. General aspect of new species shown in Figs. 1 and 2 and morphometric data presented in Table 1. Body elongate, round in cross section close to head and progressively more compressed towards caudal fin. Body in lateral view constant in depth along its whole length. Conspicuous fin-fold extending along nearly whole of dorsum, from occiput anteriorly to caudal fin posteriorly. Dorsal fin-fold deepest along caudal peduncle, fusing with caudal fin. Posterior half or third of dorsal fin-fold with small fatty bodies alongside base. Gravid females with tumescent posterior part of abdomen, with large eggs seen by transparency. Mature males often with testes seen by transparency as white opaque cloud inside posterior portion of abdomen. Ventral part of body with paired metapleural keels extending longitudinally along ventrolateral edge of trunk, from vertical through origin of pectoral fins to anterior third or fourth of caudal peduncle, posterior to anal and urogenital openings. Ventral margin of caudal peduncle with ventral fin-fold along its posterior two-thirds or three-fourths, with fatty bodies along base similar to those in dorsal fin-fold. Large conical urogenital papilla present in males (Fig. 5) and absent or very small in females. Head elongate, widest at snout (Figs. 2 and 3). Maxillary, rictal and nasal barbels short and thick, with blunt round tips and similar lengths. Internal core transparent but clearly visible in all three pairs of barbels. Maxillary barbels deflected strongly anteriorly in preserved and live specimens. Nasal barbels located closer to eyes than to anterior margin of snout. Proximal portion of rictal barbels directed straight posteriorly, but bending ventrolaterally in many preserved specimens. Nostrils minute, nearly invisible in alcohol-preserved specimens but evident in cleared and stained and SEM preparations (Figs. 3a and 6). Both nostrils in form of simple orifices, lacking occlusion valves. Anterior nostril located slightly anterior to base of internal core of nasal barbel. Posterior nostrils slightly closer to anterior margin of eye than to anterior ones. Posterior nostrils slightly closer together than anterior nostrils. Anterior and posterior nostrils united by sinusoidal ridge of integument, forming small lobe anterior to posterior nostril. Branchiostegal membranes attached to isthmus only anteriorly, their margin forming nearly continuous semicircular arc when expanded (v-shaped when collapsed), with small semicircular flap (often not visible due to shrinkage or folding) anteromesially to base of pectoral fin in ventral view (Fig. 3b), covering corresponding recess of isthmus. Branchial openings wide, each one extending from base of pectoral fin nearly to ventral midline. Profile of branchial membrane semicircular when completely

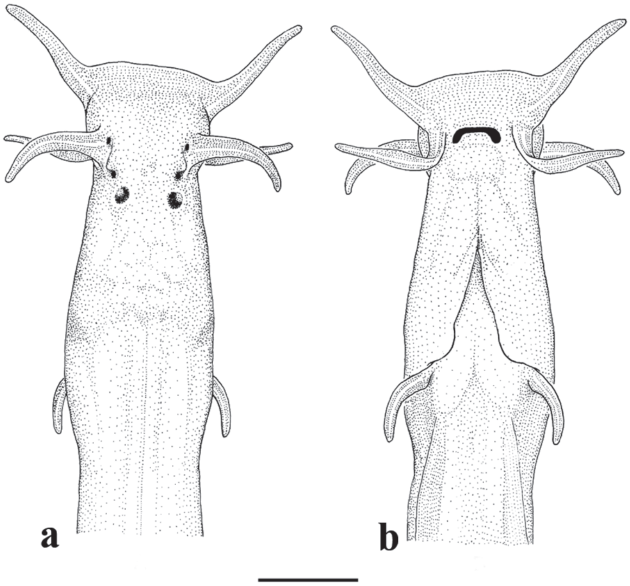

Fig. 2. Dorsal (**a**) and ventral (**b**) views of head of *Pygidianops amphioxus*, holotype, INPA 34661. Scale bar = 1 mm.

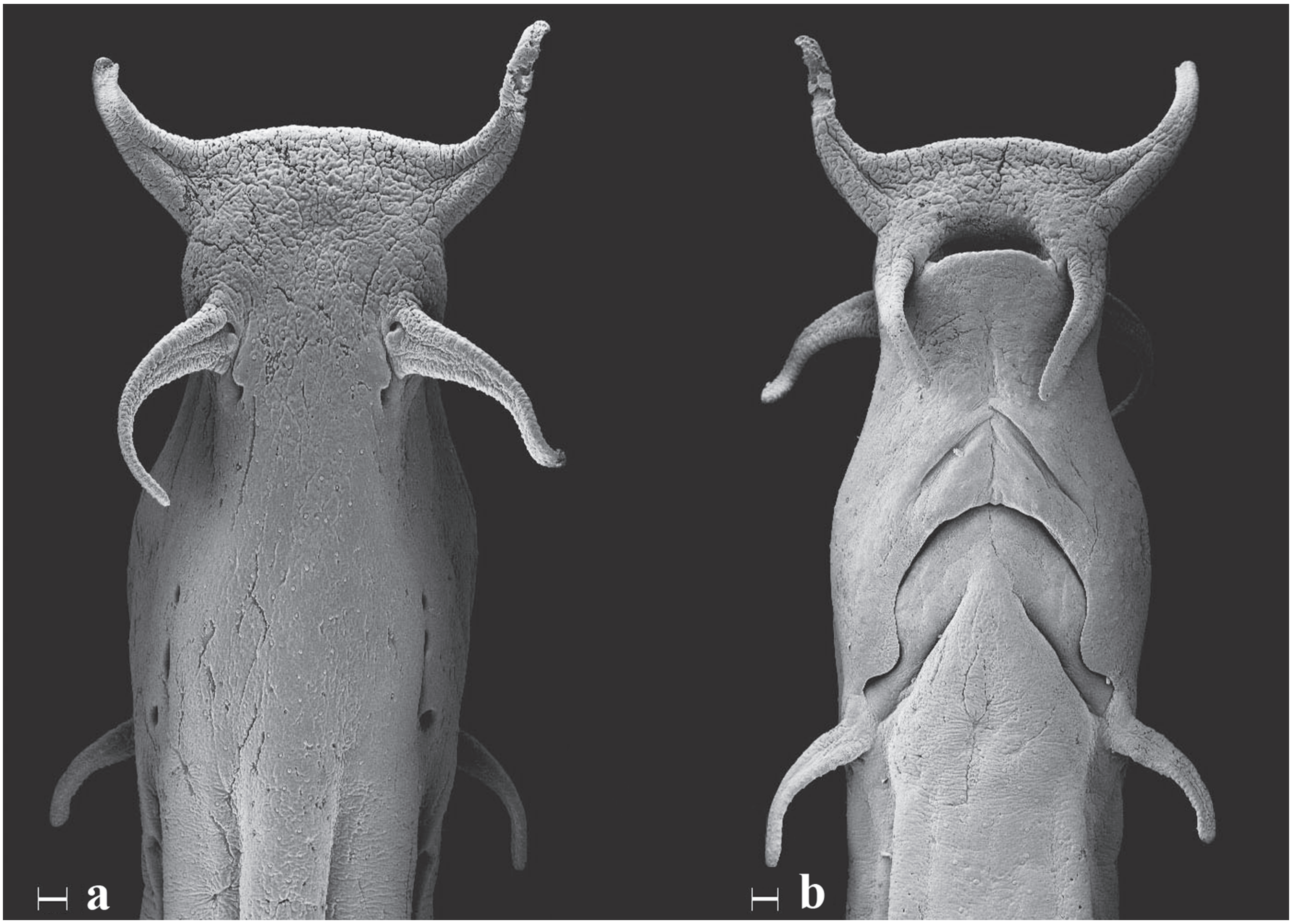

Fig. 3. Dorsal (**a**) and ventral (**b**) SEM views of the head of *Pygidianops amphioxus*, MZUSP 87676. Scale bars = 100 µm.

expanded (Fig. 3b), but often collapsed into inverted v-shape (as in holotype; see Fig. 2a) according to position of branchial basket at preservation. Eyes located at middle of HL, with well-formed lens directed antero-laterally. One paratype with eye on one side partly degenerate, or malformed. Opercular and interopercular odontodes absent. Five latero-sensory pores present on side of head (Fig. 4, top), corresponding to (anterior to posterior) infraorbital pore, preopercular canal pore, pore 1 of lateral line, pore 2 of lateral line, and terminal pore of lateral line. Short lateral line following path between two posterior pores, oriented at approximately 45 degree angle relative to body axis. Pore of axillary gland absent.

Pectoral fin short and narrow (more so towards tip), slightly curved posteriorly, resembling short barbel in external aspect. Single unsegmented and unbranched pectoral-fin ray. Anal, dorsal, pelvic and adipose fins absent. Caudal fin very small and round, continuous with caudal peduncle, with 7+6, [6+6], 6+7 or 5+6 poorly calcified rays, all unsegmented and unbranched. Only two or three procurrent caudal-fin rays dorsally and ventrally. Fold-like expansions of caudal peduncle without procurrent rays for most of their lengths. Post-Weberian vertebrae 58 (n=1) or 59 (n=4), all with well-developed neural spines and all but two anterior ones also with hemal spines (in one specimen, last free vertebra has neither spine). Single pair of pleural ribs, directed posteriorly, on first free centrum. Five branchiostegal rays.

Coloration. Dark pigmentation very reduced in preserved fish. Scattered dark chromatophores along whole of dorsum, forming two faint dorsal longitudinal stripes alongside dorsal

Table 1. Morphometric data for *Pygidianops amphioxus*, n = 15, including holotype.

	Holotype	Range	Mean
SL (mm)	25.5	22.0-30.4	25.5
	Percent of Standard Length		
TL	1.05	1.03-1.05	1.04
Body depth	0.06	0.05-0.09	0.07
Preproctal length	0.76	0.72-0.76	0.74
Caudal peduncle length	0.23	0.22-0.28	0.26
HL	0.11	0.10-0.12	0.11
	Percent of Head Length		
Head width	0.47	0.45-0.59	0.53
Snout length	0.41	0.41-0.50	0.44
Interorbital width	0.12	0.11-0.15	0.13
Internarial	0.26	0.19-0.36	0.29
Prenasal	0.25	0.24-0.35	0.29

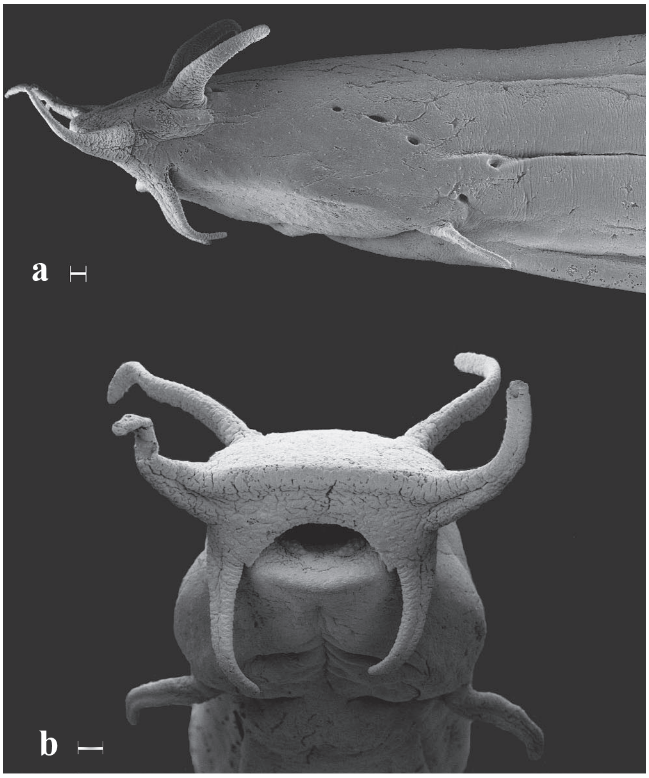

Fig. 4. Lateral (**a**) and anteroventral (**b**) SEM views of the head of *Pygidianops amphioxus*, MZUSP 87676. Scale bars = 100 µm.

fin-fold. Small faint field of melanophores dorsal to pectoral fin. Some mature females with few scattered dark fields deep inside abdominal cavity, around eggs. Head with dark brain pigment seen by transparency, forming web-like pattern. Eyes very dark, sharply visible in external aspect. Remainder of fish white, all other color differences resulting from muscle limits and different underlying tissues seen by transparency. In life the fish is light pink with a faint iridescence under direct light. Although not transparent, its general color makes it almost invisible against the sand of its natural habitat. At close range the dark eyes are evident.

Sexual dimorphism. A very large conical genital papilla is present in several specimens of *P. amphioxus* (Fig. 5) and examination of gonads has shown that all such specimens are male. The presence or absence of a hypertrophied genital papilla can be determined even in the smallest specimens examined (17.7 mm SL), as long as the urogenital region is well preserved. It is a reliable non-invasive method for sexing of specimens. Presence of a sexually-dimorphic papilla is often associated with insemination in fishes. In characiforms, where the phenomenon has been investigated in recent years, all known taxa bearing a urogenital papilla are inseminating (N. Menezes, pers. comm.; see examples in Burns & Weitzman, 2006 and Menezes *et al.*, 2009). This is indication that *P. amphioxus* is inseminating and, if confirmed, this will be the first such case in Trichomycteridae. A genital papilla has been recorded in other species of *Pygidianops* and *Typhlobelus* (*cf.* Schaefer *et al.*, 2005) and it is possible that the papilla, and its putatively associated insemination, is synapomorphic for the two genera. Hypertrophied genital papillae are not present in species of *Glanapteryx* and *Listrura*, which have either small partly concealed papillae or no papilla at all. Females of *P. amphioxus* reach larger sizes than males. In all samples available, largest specimens are always females, which also tend to be more heavily built when mature.

Distribution. *Pygidianops amphioxus* has the broadest reported distribution of any glanapterygine species yet known, spanning over 900 km in straight line (Fig. 7). Its westernmost record is the rio Daraá, tributary of the upper rio Negro, and its eastern limit is an affluent to the rio Nhamundá, a northern Amazonian tributary just west of the rio Trombetas. Within the Ducke Preserve, the species occurs in igarapé do Acará and igarapé Tinga (Soares-Carvalho, 2010), which belong to two distinct systems. The igarapé do Acará opens on the rio Tarumã, which is a tributary to the lower rio Negro; while the igarapé Tinga is part of the rio Puraquequara which opens directly into the rio Amazonas. In all cases, *P. amphioxus* is restricted to lowland terra firme rivers on the northern Amazonian versant. This suggests some association with the Guiana Shield, a link further highlighted by the close relationship of *P. amphioxus* to *P. magoi*, from the río Orinoco (see Discussion below). However, at this time it is premature to speculate further on the significance of that association. It is likely that current distributional data are still incomplete and that the species will be found in many other localities as suitable microhabitats are more thoroughly sampled.

Ecological notes. The type locality of *P. amphioxus* is the place where the species has been most closely observed by the authors. The igarapé do Acará, is a stream located inside the forest preserve Adolfo Ducke, a 10,000 ha square of protected primary forest north of the city of Manaus (between 02º55’ 03º01’S and 59º53’ 59º59’W). The preserve is covered by mostly undisturbed “terra firme” tropical rainforest, growing over sediments from the Barreiras group (Chauvel *et al.*, 1987). Until ca. 10 years ago, the preserve was largely continuous with surrounding forest, but today it is almost entirely isolated by urban growth of Manaus. The igarapé do Acará is a tributary of the rio Tarumã, itself tributary to the rio Negro. The waters of the igarapé do Acará are clear to slightly tea-stained, quite transparent (4 m visibility), highly acidic (pH 3.4-3.8) and poorly conductive (12.7 Us$_{20}$/cm). The course of the igarapé is densely shadowed by overlying forest (12.17% vertical solar light penetration), its water is moderately cool (24ºC) and highly oxigenated (6.4 mg/l). The stream-bed is mostly sandy (average granulation 0.8 mm), interrupted by rocky outcrops which form small waterfalls and rapids at many sites. Leaf litter and debris accumulate only at few spots. The average width of the stream is 4.5 m, and the average depth is 70 cm. A few pools may be up to 2.5 m deep. During rains, the

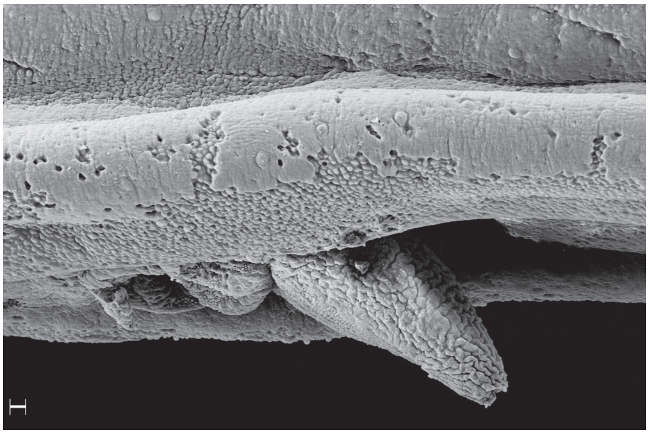

Fig.5. Ventrolateral SEM view of urogenital region in male specimen of *Pygidianops amphioxus*, MZUSP 87676. Anterior to left. Scale bar = 20 µm.

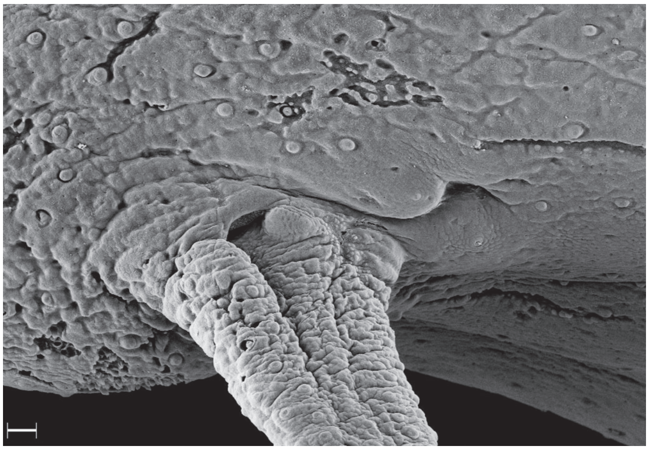

Fig. 6. Dorsal SEM view of left nostrils and respective base of nasal barbel of *Pygidianops amphioxus*, MZUSP 87676. Anterior to left. Scale bar = 30 µm.

water may raise up to 1 m beyond its normal level, but only for a short period of time (less than 24 hours). The current speed is modally 1 m/4 sec, but varies markedly according to sector, from very slow pools to fast running rapids. *Pygidianops amphioxus* is the only trichomycterid yet found in the igarapé do Acará, although at least 36 other fish species occur therein, three of which (*Gymnorhamphichthys rondoni*, *Imparfinis pristos* and *Characidium pteroides*) in the same microhabitat as the new species.

Fewer ecological data are available for the rio Preto da Eva locality, which is a site heavily impacted by human activity. The stream in the sector visited is less rocky and the water murkier than in the Ducke Preserve, while the riparian vegetation is mostly shrubby, rather than dense forest. The two latter factors seem to be due to deforestation and the presence of a dirt road crossing the stream. However, the microhabitat favored by *P. amphioxus* seems to be similar to that in the Ducke preserve, with obvious preference for the few shaded sectors of the stream. At rio Preto da Eva, *Stauroglanis gouldingi*, an undescribed species of *Paracanthopoma* and *Ituglanis* sp. are other trichomycterids co-occurring with *P. amphioxus*.

In every locality, *P. amphioxus* is an interstitial inhabitant of the sandy sectors of streams. It was collected in the superficial 20 cm of sand, in fast flowing portions, 30-60 cm in depth. The distribution of individuals seems to be spotty, with a preference for submerged sand banks immediately below small waterfalls or at steep turns of the stream course. Collecting was done by scooping large amounts of sand in a fine-mesh seine, and then looking for trapped fish. The choice of sites to be seined was done either randomly in suitable microhabitats, or by aiming at spots where fish were seen (by underwater observation) to bury after being dislodged by disturbing the sand. The fish moves extremely fast amidst submerged sand, but becomes immobilized as soon as the water drains through the mesh and the sand grains amalgamate. When hand-freed from the sand, small specimens move slowly in undulating movements over the drained substrate, resembling large aquatic nematodes. Larger specimens tend to wriggle frantically in more normal catfish manner. Despite their delicate aspect, the fish is actually quite tough to the touch.

Underwater observation of live *P. amphioxus* in its natural environment occurred only during careful disturbance of its natural microhabitats, by slowly running fingers through the superficial layer of sand. And even so, only for a fraction of a second before it darted again into the sand. Despite six hours of underwater observation by both authors, the fish has never been observed otherwise, either during the day or night. It seems to us that *P. amphioxus* never leaves the sand in normal conditions.

Pygidianops amphioxus is different from most sand-dwelling fishes, which bury in the sand by making jerky body movements and then stay close to the surface or with part of their head emerging from the sand. The new species, contrastingly, seems to hide deep in the sand, and to do so in a remarkably effortless manner. To an underwater observer, the fish looks like it dives, rather than buries, into the sand.

Before preservation, the captured fish were placed in a water-filled plastic bag, where they went straight to the bottom to hide amongst the few available sand grains. In the absence of sand, the fish seems to be unable to maintain proper resting balance, and lies on its side. If disturbed in those circumstances, it darts in convulsive eel-like movements for a few moments before dropping again to the bottom.

Pygidianops amphioxus probably feeds upon the tiny interstitial invertebrate fauna of its microhabitat. Gut contents contain many small sand grains, along with unidentified arthropod remains and other finely-macerated organic debris. Sand grains in the gut (in this case considerably larger) are also visible in the cleared and stained specimen examined of *P. eigenmanni*. It seems like in the process of capturing its tiny prey, species of *Pygidianops* also swallow some of the surrounding sand. They possibly also take nutrition from the organic layer surrounding ingested sand grains (biofilm). In

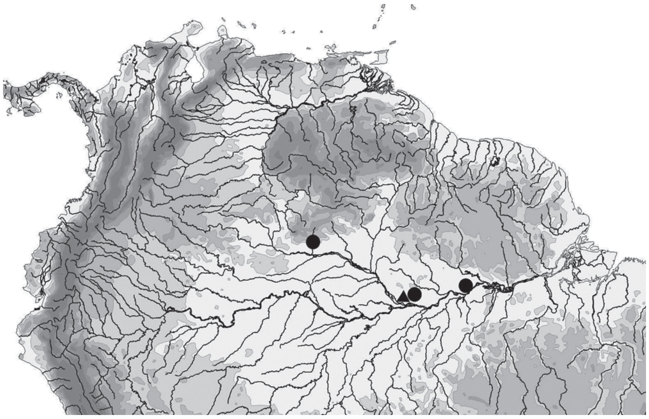

Fig. 7. Northern South America with the distribution of *Pygidianops amphioxus*. Triangle represents type locality.

either case, it seems that *P. amphioxus* feeds while buried in the sand, which further supports the view that those fishes never leave the sand as part of their normal activities.

The material available includes several mature females with large eggs seen by transparency, indicating that the specimens studied are adult individuals. The eggs in each ovary are disposed roughly in single file, but the two rows of eggs are arranged in a partly imbricate manner along the abdominal cavity. This arrangement seems to be related to the minute size of the fish and its elongate shape, which result in eggs that are large relative to the internal space in the abdominal cavity. Similar space-saving strategies are common in ovaries of various unrelated paedomorphic taxa, such as some phengodid beetles (Costa *et al.*, 1999). No small juveniles were caught, possibly because they are so small as to escape the collecting gear employed. Soares-Carvalho (2010) concluded that *P. amphioxus* reproduces throughout the seasonal cycle, with an increased rate in the dry season. The sex ratio in the species is approximately 50/50.

Etymology. The specific name, a noun in apposition, refers to the cephalochordate amphioxus (a common name that applies to Recent cephalochordates in general, now mostly included in the genus *Branchiostoma*), in allusion to obvious similarities in body shape and superficial aspect.

Remarks. Little morphological divergence exists among the four populations known of *P. amphioxus*. Specimens from the rio Daraá, on average, are slightly darker along the dorsum than those of other populations. Individuals from the rio Preto da Eva have the articular process of the palatine somewhat more produced than those from the Ducke Preserve (specimens of other populations have not been examined for osteology). Such differences are small and fit expected variation normally observed within single species of glanapterygines. Specimens from the igarapé Jamari and rio Daraá have not been designated as types because of their outlying localities and relatively limited study material at this time.

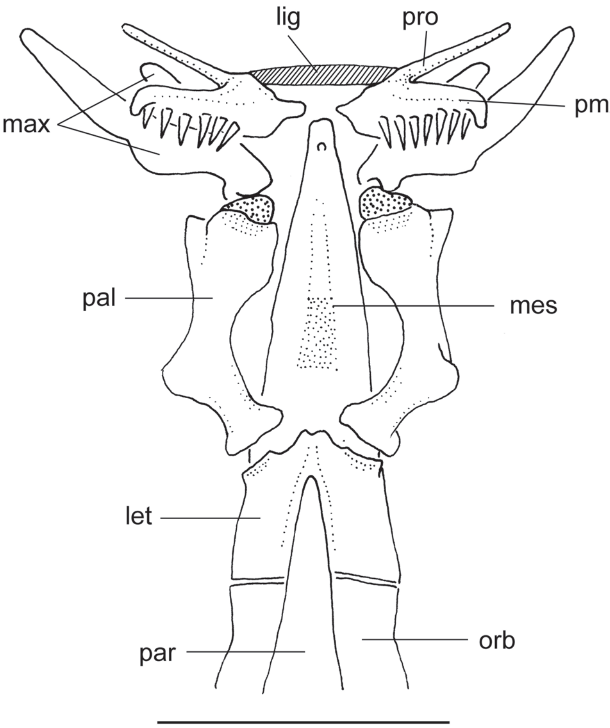

Fig. 8. Anterior portion of jaws and associated structures in *Pygidianops amphioxus*, MZUSP 87676. Ventral view. Larger stippling represents cartilage. Hatching represent interpremaxillary ligament. let (lateral ethmoid), lig (ligament), max (maxilla), mes (mesethmoid), orb (orbitosphenoid), pal (palatine), par (parasphenoid), pmx (premaxilla), pro (process on premaxilla). Scale bar = 0.5 mm.

Discussion

In contrast to all previously-known species of *Pygidianops* and *Typhlobelus*, *P. amphioxus* does not fit obviously into one or the other genus on the basis of traditional well defined differences in body shape and other external-morphological traits. The species deviates markedly from the general aspect otherwise seen in species of the two genera and a more detailed comparative analysis is necessary for the correct determination of its generic placement. Data additional to those traditionally used to diagnose glanapterygine genera strongly indicate that the new species forms a monophyletic group with those currently included in the genus *Pygidianops*. Evidence for that is listed and explained below as numbered synapomorphies.

1- Premaxilla with laterally-directed process inserted dorsally close to the medial end of bone.

The toothed premaxilla in *Pygidianops* has a long process originating close to its mesial end, directed laterally and overlapping an anterior process of the maxilla (Fig. 8). The processes and the maxillary-premaxillary connection thus

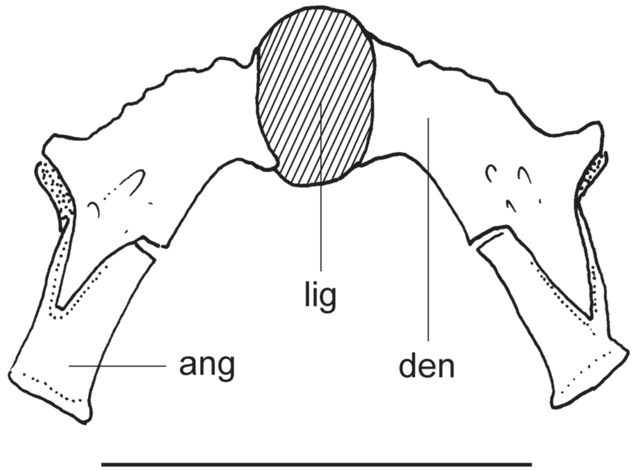

Fig. 9. Lower jaws of *Pygidianops amphioxus*, MZUSP 87676, ventral view. Hatching represents intermandibular ligament. ang (anguloarticular), den (dentary), lig (ligament). Scale bar = 1 mm.

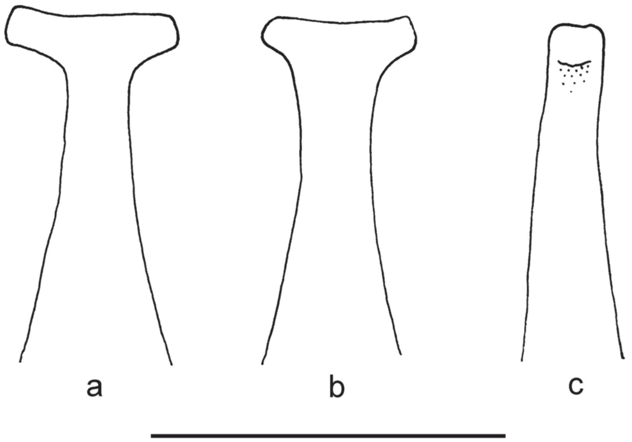

Fig. 10. Anterior portion of mesethmoid in species of *Pygidianops*: (**a**) *P. cuao*, paratype, MZUSP 81769; (**b**) *P. eigenmanni*, paratype, CAS 11121; (**c**) *P. magoi*, paratype, MZUSP 84304. Scale bar = 0.5 mm.

formed are unique among trichomycterids and other loricarioids. The shape of the process varies in different species of *Pygidianops*. It is longest in *P. cuao*, where it is also almost perfectly straight, extending well beyond the lateral limit of the premaxilla. In *P. amphioxus* and *P. magoi* the process is mostly straight but angled at its basal portion at the attachment of a ligament linking the process with the mesethmoid (in *P. magoi*) or uniting the two premaxillary processes (in *P. amphioxus*). Finally, *P. eigenmanni* is the only species in which the process is gently curved.

2- Lower jaw rotated ventrally.

The lower jaw in *Pygidianops* is positioned so that the side that is normally lateral in other trichomycterids and catfishes is shifted to face ventrally. Because of the modified orientation of the lower jaw, the distal portion of the coronoid process is strongly curved dorsally, so that its distal tip reaches the position necessary to connect the lower jaw with the upper. Such positional changes also result in the dentary teeth being directed anteriorly. None of these modifications are seen in *Typhlobelus*, where the lower jaw has a normal orientation with the lateral surface directed mostly laterally, the coronoid process is mostly straight, and the dentary teeth are directed anterodorsally.

3- Symphyseal ligament hypertrophied.

In all species of *Pygidianops* the symphysis of the lower jaw is enlarged and connected by a markedly hypertrophied ligament (Fig. 9). The articular facets on the mesial tip of each dentary are expanded and the intervening ligament bulges beyond the bony margins of the mandibular rami, being approximately globose in shape. Despite the obviously reinforced symphyseal connection, the actual bony portions of the mandibular rami are distantly positioned, so that the resulting articulation is strong yet flexible. Such series of modification in the symphyseal articulation are unique to species of *Pygidianops*.

The closest relative of *P. amphioxus* seems to be *P. magoi*. The two species share a unique modification of the mesethmoid, unparalleled among trichomycterids. Their mesethmoid cornua are completely absent (this was previously proposed as an autapomorphy for *P. magoi* by Schaefer *et al.*, 2005), so that the bone ends as a blunt rod in dorsal view (Figs. 8 and 10c). Additionally, the tip of the mesethmoid is bent dorsally at a nearly 90-degree angle relative to the rest of the bone and to the longitudinal axis of the skull (Fig. 11). Slight excavations exist on each side of the upturned portion, immediately ventral to its tip. There is also a second and much smaller process directed ventrally. Such a series of modifications of the mesethmoid are not present in other glanapterygines (Fig. 10a and b), which have well defined mesethmoid cornua (expanded into a roughly discoidal shape in *Typhlobelus*), not bent dorsally and lacking a ventral process, similar in those respects to the generalized condition in other trichomycterids. The palatine in *P. amphioxus* and *P. magoi* is also uniquely distinctive in having its articulation with the neurocranium by means of a well-defined produced posterior process (Fig. 8). This morphology is considered apomorphic since in other species of *Pygidianops* and remaining glanapterygines the articular facet of the palatine is not markedly produced from the main body of the bone, a situation seen also in most other trichomycterids.

As seen above (see synapomorphy nº 1 for *Pygidianops*), the shape of the dorsal (laterally-directed) premaxillary process in *P. amphioxus* and *P. magoi* differs from that in other species of the genus in being straight-angulate (*vs.* almost entirely straight in *P. cuao* and gently curved in *P. eigenmanni*). While this may provide additional evidence for a relationsip between the two species, it is impossible at this

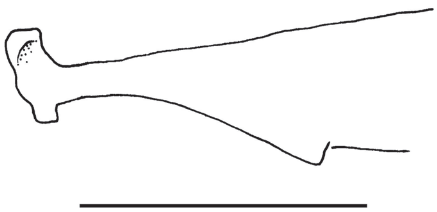

Fig. 11. Lateral view of mesethmoid of *Pygidianops amphioxus*, INPA 12427. Anterior to left. Scale bar = 0.5 mm.

point to confirm its status as a synapomorphy, because the process is absent in outgroups. Additional support for a *P. amphioxus* + *P. magoi* clade comes from the absence of anal fin in both taxa (a trait previously proposed as an autapomorphy for *P. magoi* by Schaefer *et al.*, 2005: 20). All other species of both *Pygidianops* and of *Typhlobelus* have anal fins, as do species of *Listrura*. *Glanapteryx* is the only other glanapterygine that lacks an anal fin. Within the phylogeny currently known for the subfamily (de Pinna, 1989), the loss of anal fin occurred convergently in *Glanapteryx* and in the clade formed by *P. amphioxus* plus *P. magoi*. Finally, *P. amphioxus* and *P. magoi* are the only species in the genus with a single pair of pleural ribs. The evidence provided by this character is circumstantial, however, because species of *Glanapteryx* and *Typhlobelus* also have a single pair of ribs (or no ribs in *T. guacamaya*).

A few characters were identified as putative autapomorphies for *P. amphioxus*. The narrow continuous ligament connecting the dorsal processes of the premaxillae (Fig. 8) is unique in the genus. In other species of the genus, possibly homologous ligaments connect each process with the tip of the mesethmoid. The attachment site of the ligament on the premaxillary process is similar to that in *P. amphioxus*, and it seems likely that the single ligament in the latter was formed by fusion of the two separate ligaments seen in other species of *Pygidianops*, with the concomitant loss of the mesethmoid cornua primitively located between the two premaxillae. The shape of the opercle in *P. amphioxus*, with a hypertrophied ascending process (Fig. 12), is also unique to the species. In other species of *Pygidianops*, as in those of *Typhlobelus*, the opercle is narrow and elongate, with the ascending process either absent or vestigial. Another unique feature of *P. amphioxus* among species of *Pygidianops* is the lack of the lacrimal bone (infraorbital one). All other species in the genus have a long lacrimal. This character, however, cannot be decisively determined as autapomorphic because species of *Typhlobelus* also lack that bone.

The revised diagnosis below includes some novel differences found between *Pygidianops* and *Typhlobelus* that require comment. In internal anatomy, the most dramatic distinctions are found in the ventral portion of the branchial skeleton. Species of *Pygidianops* have a complete series of ventral branchial-arch elements, conforming in that aspect to the condition in generalized trichomycterids. They have three well-differentiated basibranchials (two anterior ones ossified and the posterior one cartilaginous), three pairs of ossified hypobranchials and five pairs of ossified ceratobranchials (Fig. 13; *cf.* also Baskin, 1973, fig. 84). Species included in *Typhlobelus*, contrastingly, have only the ceratobranchials well differentiated, lacking nearly all other elements of the ventral branchial skeleton. The hypobranchial and basibranchial series are missing or reduced to irregular streaks of cartilage, with the posterior cartilaginous basibranchial, even though reduced in size, as the only remaining individualized element. Such reductions are evidently apomorphic and, within siluriforms, paralleled only in members of the subfamily Vandeliinae, a clearly homoplastic occurrence in view of the phylogenetic distance between vandelliines

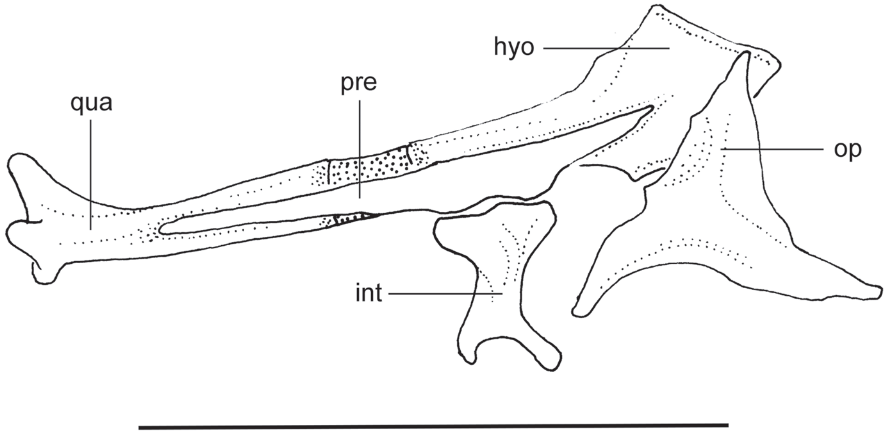

Fig. 12. Suspensorium of *Pygidianops amphioxus*, MZUSP 87676. Left side, anterior to left. Larger stippling represents cartilage. hyo (hyomandibula), int (interopercle), op (opercle), pre (preopercle), qua (quadrate). Scale bar = 1 mm.

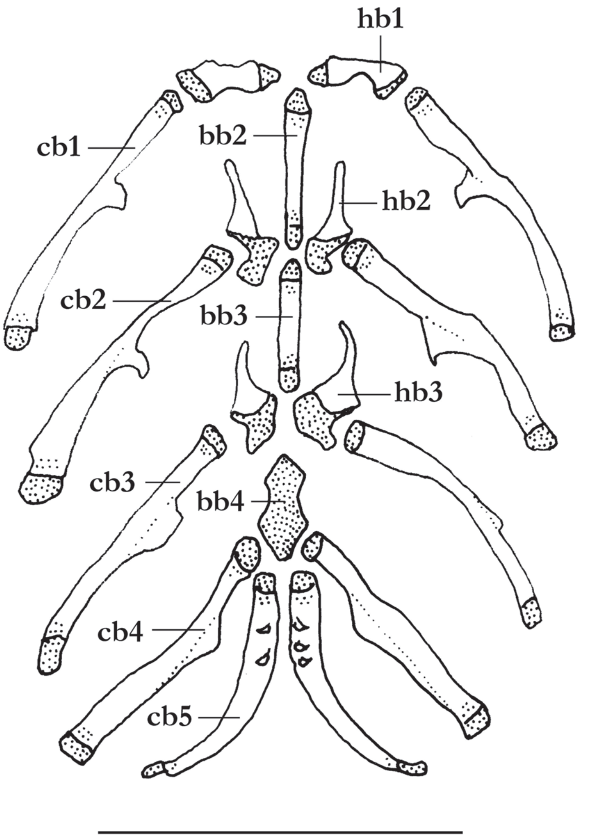

Fig. 13. Ventral portion of branchial arches of *Pygidianops amphioxus*, MZUSP 87676, dorsal view. Stippling represents cartilage. bb2-4 (basibranchial 2 to 4), cb1-5 (ceratobranchial 1 to 5), hb1-3 (hypobranchial 1 to 3). Scale bar = 0.5 mm.

and *Typhlobelus*. In Vandelliinae, the branchial skeleton reduction is associated with the liquid feeding (hematophagy) seen in all species of the subfamily. Feeding habits in species of *Typhlobelus* are not known, but they are certainly not hematophagous. Their similar branchial reductions suggest that species of the genus may have a most unusual food source, yet unknown and markedly different from that of *Pygidianops*. Such considerations are further highlighted by their reduced oral dentition, which can reach total lack of teeth in the upper jaw of *T. guacamaya*.

As noticed by Schaefer *et al.* (2005), the palatine differs markedly in *Pygidianops* and *Typhlobelus*. In the former, the palatine is large and oriented in parallel to the neurocranium (Fig. 8), traits that conform to conditions commonly found in other trichomycterids and remaining siluriforms. In *Typhlobelus*, the palatine is small and club-shaped, with its longest axis oriented obliquely, sometimes nearly at a right angle, relative to the neurocranium. This is a condition almost unique among catfishes.

In the suspensorium, the most evident distinction between *Pygidianops* and *Typhlobelus* is that the posterior margin of the hyomandibula in the latter has a large process directed postero-ventrally, roughly parallel to the opercle. The posterior margin of the hyomandibula in *Pygidianops* lacks any processes (Fig. 12).

Pygidianops Myers, 1944

Type species: *Pygidianops eigenmanni*, Myers, 1944.

Revised diagnosis. Glanapterygine trichomycterids uniquely diagnosed by a hypertrophied symphyseal joint and associated ligament in the lower jaw; an elongate, laterally-directed, process on the dorsal surface of the premaxilla; a rotated lower jaw, where the surface normally facing laterally in other glanapterygines is instead directed ventrally. Further distinguished from its closest relative, *Typhlobelus*, by the snout relatively short, not prolongued into a duck-bill shape; the presence of numerous teeth on each premaxilla (*vs*. 1-4); the presence of well-differentiated (and partly ossified) basibranchials and hypobranchials (*vs*. elements mostly undifferentiated or absent); the palatine large and oriented in parallel to the neurocranium (*vs*. palatine small, club-shaped and oriented obliquely to the neurocranium); the posterior margin of the hyomandibula lacking a process (*vs*. large pointed process posteriorly on posterior margin of hyomandibula); and the premaxilla articulating with the anterior end of the mesethmoid (*vs*. articulating with the shaft of the mesethmoid). Further distinguished from *Listrura* and *Glanapteryx* by the presence of metapleural keels along the edges of abdomen, the reduction or lack of dark integument pigmentation and the presence of a long dorsal-fin fold extending along most of dorsal margin of body. Further distinguished from *Listrura* by the short pectoral fin, the absence of opercular and interopercular odontodes and the absence of dorsal fin.

Included species: *P. eigenmanni* Myers, 1944; *P. cuao* Schaefer, Provenzano, de Pinna & Baskin, 2005; *P. magoi* Schaefer, Provenzano, de Pinna & Baskin, 2005; and P. *amphioxus*, new species.

Comparative Material Examined. *Glanapteryx anguilla*, MZUSP 36530, 19 (2 c&s), 33.7-63.2 mm SL, Brazil, Amazonas, rio Negro, igarapé São João, near Tapurucuara, 00°24'S 65°02'W. *Glanapteryx niobium*, INPA 12421, holotype, 55.3 mm SL, Brazil, Amazonas, Pico da Neblina National Park, Morro dos Seis Lagos, lago Esperança, 00°17'N 66°41'W. *Listrura camposi*, MZUSP 95189, 17 (3 c&s),19.8-46.2 mm SL. *Listrura nematopteryx*, MZUSP 36974, holotype, 26.9 mm SL, Brazil, Rio de Janeiro, Piabetá, marsh which joins Ribeirão Imbariê (tributary to rio Estrela), near 58 km mark of old road to Petrópolis, 22°36'36"S 43°11'26"W; MZUSP 36975, 12, paratypes, 16.3-36.7 mm SL, collected with holotype; MZUSP 37138, 8 (c&s), ca. 14-28 mm SL, collected with holotype. *Listrura picinguabae*, MZUSP 106807, 6 (4 c&s), 33.1-41.7 mm SL, Brazil, São Paulo, Ubatuba, coastal creek at Picinguaba. *Listrura tetraradiata*, MNRJ 19064, 10 (2 c&s), 15.0-44.2 mm SL, Brazil, Rio de Janeiro, Saquarema, Palmital, Hotel Fazenda Barra da

Castelhana. *Pygidianops cuao*, MZUSP 81769 (ex-AMNH 232970), 4 (1 c&s), paratypes, 13.4-19.0 mm SL, Venezuela, Amazonas, río Cuao at Raudal Guacamaya, 8.1 miles upstream from Raudal El Danto, 05°07.71'N 67°31.53'W; MZUSP 82103, 5 (1 c&s), 13.4-19.0 mm SL, paratypes, same data as MZUSP 81769; MZUSP 82104, 3, paratypes, 10.6-18.4 mm SL, Venezuela, Estado Amazonas, río Cuao at Isla de Cielo, 21.3 km upstream from Raudal El Danto, 05°11.01'N 67°31.11'W. *Pygidianops eigenmanni*, CAS 11121, 2 (1 c&s), paratypes, 13.3-18.5 mm SL, Brazil, Amazonas, São Gabriel da Cachoeira, rio Negro, rock pools below São Gabriel rapids. *Pygidianops magoi*, MZUSP 84303, 2, paratypes, 15.0-15.3 mm SL, Venezuela, Delta Amacuro, río Orinoco at Puerto Cabrian, 08°34'48"N 62°15'54"W; MZUSP 84304, 1 (c&s), paratype, 11.4 mm SL, Venezuela, Bolívar, río Orinoco, 08°18.3'N 62° 56.1'W; MZUSP 84306, 1ex, paratype, 15.7 mm SL, Venezuela, Delta Amacuro, río Orinoco downstream from Puerto Cabrian, 08°34'N 62°15'W. *Typhlobelus guacamaya*, MZUSP 81770, 3 (1c&s), paratypes, 23.3-25.6 mm SL, Venezuela, Amazonas, río Cuao, at Raudal Guacamaya, 13km upstream from Raudal El Danto, 05°07.71'N 67°31.53'W. *Typhlobelus lundbergi*, MZUSP 84305, 3 (1c&s), paratypes, 20.8-22.0 mm SL, Venezuela, Bolivar, río Orinoco, 08°18'18"N 62°56'06"W. *Typhlobelus macromycterus*, MNRJ 12129, holotype, 21.6 mm SL, Pará, rio Tocantins, near city of Tucuruí. *Typhlobelus cf. macromycterus*, MZUSP 106846, 5 (1 c&s), 24.1-27.1 mm SL, Brazil, Pará, Belo Monte, paraná in rio Xingu, 03°06'06"S 51° 42'49"W. *Typhlobelus ternetzi*, CAS 11119, 2 (1c&s), paratypes, 22.3 mm SL, Brazil, Amazonas, São Gabriel da Cachoeira, rio Negro, rock pools below São Gabriel rapids. *Typhlobelus* sp., INPA 12929, 7 (2 c&s), 20.0-30.1 mm SL, Brazil, Pará, Senador José Porfírio, rio Xingu at Arroz Cru. Representatives examined of other Trichomycteridae and loricarioids are listed in de Pinna (1992).

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